Evolutionary Systematics. 7 2023, 257–266 | DOI 10.3897/evolsyst.7.102578

PENSOFT

EVOLUTIONARY SYSTEMATICS

# A new species of groundsnake genus *Atractus* Wagler, 1828 (Serpentes, Dipsadidae) from the Peruvian Andes revealed by unequivocal morphological characters

Paulo R. Melo-Sampaio[1], Pablo J. Venegas[2,3]

1 *Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil*

2 *Rainforest Partnership, 4005 Guadalupe St., Austin, TX 78751, USA*

3 *Instituto Peruano de Herpetología (IPH), Lima, Peru*

*https://zoobank.org/9DE78DA4-B256-4B36-AFBB-5910BBA16B6E*

Corresponding author: Paulo R. Melo-Sampaio (prmelosampaio@gmail.com)

Academic editor: Oliver Hawlitschek ♦ **Received** 23 February 2023 ♦ **Accepted** 15 May 2023 ♦ **Published** 9 August 2023

## Abstract

Based on an exhaustive revision of external morphological characters we describe a new species of *Atractus* from the humid montane forest of the Andes of northern Peru, Cajamarca department, occurring at elevations of 1641 to 2161 m. This new species was misidentified as *A. gigas* in the literature and for more than a decade represented the southernmost record of the that species. In the absence of molecular data and limited by a small sample, we use some underreported characters in the genus *Atractus* such as the presence of apical pits. Thus, the combination of apical pits as well as other characters mentioned in the literature (i.e., head scutellation and number of subcaudals) distinguishes the Peruvian population from *A. gigas*, and strongly supports the morphological separation of this taxon from the rest of its congeners.

## Key Words

Apical pits, Andes, endemism, morphology, scales, tubercles

## Introduction

During last five years, the taxonomy of the genus *Atractus* has improved notably with molecular data leading to systematization of this fascinating group of cryptozoic snakes in the tree of life (Arteaga et al. 2017; Melo-Sampaio et al. 2019; Murphy et al. 2019; Jowers et al. 2021; Melo-Sampaio et al. 2021a; Arteaga et al. 2022). Those studies collectively led to an increase in diversity with seven new species "molecular-based" or "phylogenetically positioned" as well as generating relevant new data for poorly known ones. On the other hand, in the same timespan morphological data was also critical to shedding light on eight new species (Passos et al. 2016; Melo-Sampaio et al. 2019; Meneses-Pelayo and Passos 2019; Passos et al. 2019a, b; Melo-Sampaio et al. 2021a). Faced with this encouraging scenario of discoveries, Passos et al. (2022) argued that phylogenies are complements equally important when available, but data integration should be solid enough in the test of hypotheses and grounded by multiple lines of evidence.

Despite having a usually secretive habit that makes sighting by humans difficult, many species of *Atractus* are relatively large, reaching more than 600 millimeters (Silva-Haad 2004; Tolhurst et al. 2010). Among the largest species of the genus are *A. albuquerquei* Cunha & Nascimento, 1983, *A. atlas* Passos, Scanferla, Melo-Sampaio, Brito & Almendáriz, 2019, *A. gigas* Myers & Schargel, 2006, *A. major* Boulenger, 1894, *A. obesus* Marx, 1960, *A. pachacamac* Melo-Sampaio, Passos, Prudente, Venegas & Torres-Carvajal, 2021, *A. serranus* Amaral, 1930, *A. touzeti* Schargel, Lamar, Passos, Valencia, Cisneros-Hereda & Campbell, 2013, *A. trihedrurus* Amaral, 1926, and *A. ukupacha* Melo-Sampaio, Passos, Prudente, Venegas & Torres-Carvajal, 2021.

Copyright *Paulo R. Melo-Sampaio & Pablo J. Venegas*. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Descriptions of "giant" *Atractus* in the Andes region are uncommon and primarily based on small samples (Marx 1960; Passos et al. 2019a). *Atractus gigas* was described based on a single specimen from Bosque Protector Río Guajalito, between Quito and Santo Domingo, Pichincha, Ecuador (Myers and Schargel 2006). Later, Tolhurst et al. (2010) found the first live specimen in primary cloud forest, Bosque Protector Santa Lucía, extending the distribution 48 km NE from the type locality. Passos et al. (2010), provided new information about phenotypic variation based on 11 specimens from Ecuador and Peru, highlighting that those Peruvian specimens have a smaller number of subcaudals than Ecuadorian specimens of *Atractus gigas*. Additionally, they have more supralabials, more infralabials, and four infralabials contacting chinshields. Despite these significant differences in characteristics between the Ecuadorian and Peruvian populations, Passos et al. (2010) argued that they represented the first occurrence of one *Atractus* species (*A. gigas*) on both sides of the Andes. Recently Arteaga et al. (2022) properly raised concerns about the status of *Atractus gigas* along the eastern versant of the Andes. They argue that scutellation and ontogenetic variation between Ecuadorian and Peruvian specimens are easily diagnosable and suggest re-identification as *Atractus atlas* or perhaps as a new species. Analysis of other species occurring along the Andes led us to exhaustively verify diagnostic morphological features hitherto unknown in some *Atractus* and allows us to describe the Peruvian species previously confused with *A. gigas* as a new species.

## Materials and methods

### Morphology, species boundaries and presentation rationale

Terminology for cephalic shields follows Savage (1960) and Peters (1964), whereas ventral and subcaudal counts follow Dowling (1951). Body proportions were measured from snout–vent length (SVL) and tail length (TL), with a flexible ruler to the nearest 1 mm. We used a Mitutoyo digital calliper to the nearest 0.1 mm in measurement of head scalation. Measurements and descriptions of paired cephalic scales are strictly based on the left side of the head. Dentition was examined in situ under an Olympus stereomicroscope through a narrow lateromedial incision between the supralabials and the maxillary arch. After removing tissues covering the maxillary bone, we counted the number of teeth or empty sockets. Colouration was described following a standardized catalogue (Köhler 2012).

We follow Melo-Sampaio et al. (2021a) in focusing our comparisons to species that meet at least one of the following criteria: (a) species with close phylogenetic relationships, recovered in previous studies; (b) sympatric or parapatric taxa presenting similar colour pattern, scutellation and morphometric features; (c) species previously confused with new species in the literature or scientific collections (e.g., *Atractus gigas* in Passos et al. 2010). We examined 145 specimens of *Atractus* from Brazil, Ecuador, and Peru for comparative purposes (listed in Appendix 1) housed in the División de Herpetología, Centro de Ornitología y Biodiversidad (**CORBIDI**), División de Herpetología, Museo Ecuatoriano de Ciencias Naturales (**DHMECN**), Fundación Herpetológica Gustavo Orcés (**FHGO**), Museo de la Escuela Politecnica Nacional (**MEPN**), Museo de Zoología, Pontificia Universidad Católica del Ecuador (**QCAZ**), Museo de Historia Natural, Universidad San Marcos (**MUSM**), Museu de Zoologia, Universidade de São Paulo (**MZUSP**), Museu Paraense Emílio Goeldi (**MPEG**), Setor de Herpetologia, Museu Nacional (**MNRJ**), and we received photos of specimens housed in Museum für Naturkunde (**ZMB**), Zoologisches Forschungsmuseum Alexander Koenig (**ZFMK**) and American Museum of Natural History (**AMNH**). The sex was determined by verifying presence-absence of hemipenes through a ventral incision at the base of the tail, except when the hemipenis was previously everted. Juveniles were unsexed.

## Taxonomy

### *Atractus paulus* sp. nov.

https://zoobank.org/642A84FE-4FBA-4777-B1A3-F028AFC15A79

Figs 1–3

*Atractus gigas* non Myers & Schargel, 2006; Passos et al. 2010: 74. Melo-Sampaio et al. 2021a: 747; Appendix 1.

**Type material.** ***Holotype.*** CORBIDI 877 adult female from Peru, Cajamarca Department: San Ignacio Province, Namballe District, Alto Ihuamaca (05°11'41.16"S, 79°05'2.27"W, 1641 m), collected by Maik Dobiey on 26 August 2008.

***Paratype.*** ZFMK 89147 juvenile from Peru, Cajamarca Department, San Ignacio Province, Namballe District, El Chaupe (05°14'8.88"S, 79°06'16.2"W, 2161 m), collected by Maik Dobiey on 25 August 2008.

**Diagnosis.** *Atractus paulus* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 17/17/17 with apical pits near cloaca; (2) postoculars two; (3) loreal moderately long, contacting second to fourth supralabials; (4) temporal formula usually 1+2; (5) supralabials eight, fourth and fifth contacting eye; (6) infralabials eight, first four contacting chinshields; (7) maxillary teeth eight; (8) gular scale rows usually four; (9) preventrals four; (10) ventrals 166–167 in females, condition in males unknown; (11) subcaudals 26 in females, condition in males unknown; (12) in preservative, dorsum yellow ochre; (13) ventral surface of body mostly black with scattered inconspicuous cream marks in juveniles, uniform brown in adults; (14) maximum body size 830 mm SVL in females; (15) tail size moderately short in females (9.1–13.6% SVL); (16) midbody diameter 18.0–27.3 mm (Figs 1–3).

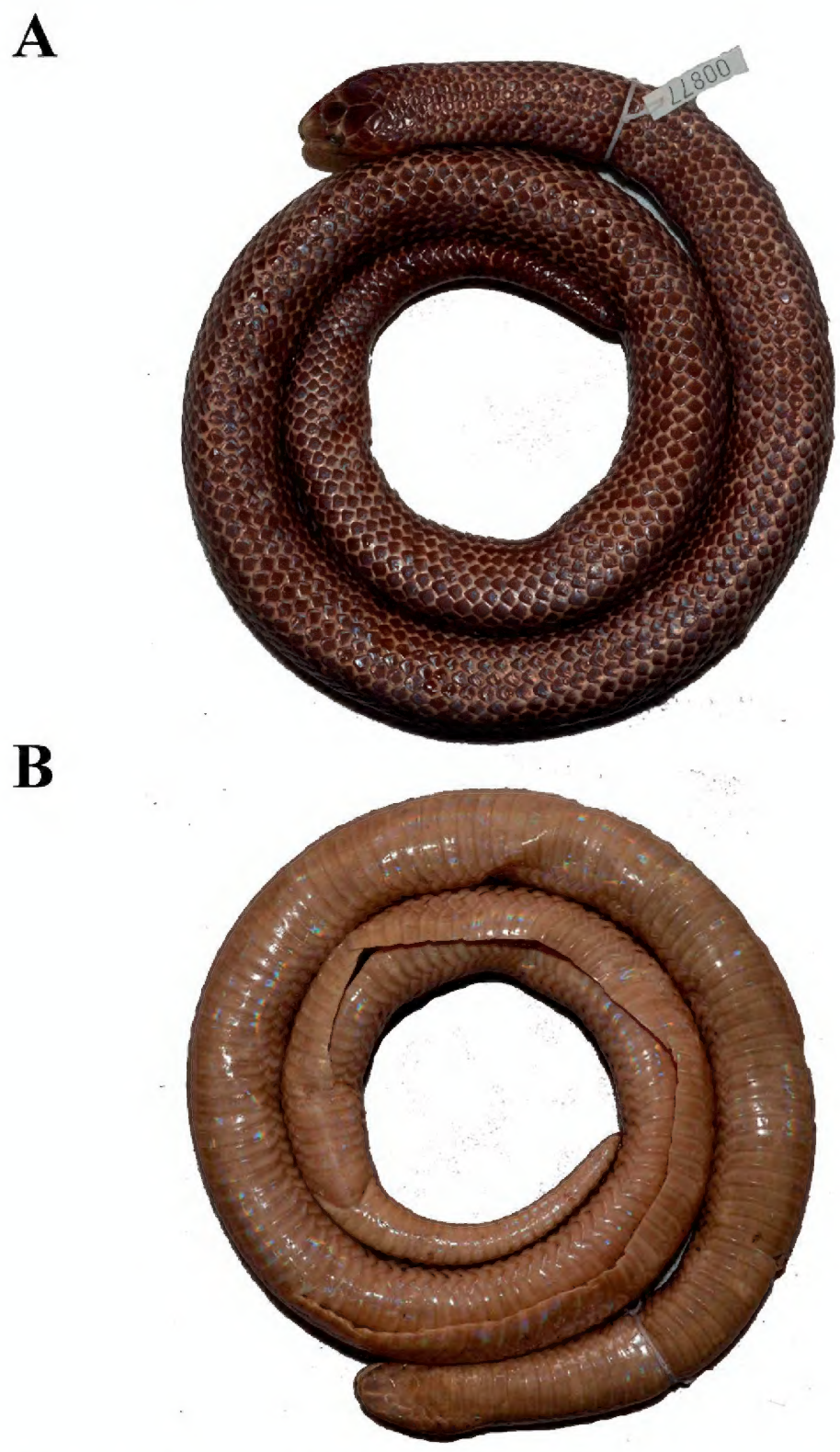


**Figure 1.** Dorsal (**A**) and ventral (**B**) view of *Atractus paulus* holotype CORBIDI 877.

**Comparisons.** Among all 150 congeners known to date (Uetz et al. 2023) *Atractus paulus* shares with only eight species a SVL larger than 600 mm: *A. atlas* Passos, Scanferla, Melo-Sampaio, Brito & Almendariz, 2019, *A. gigas* Myers & Schargel, 2006, *A. obesus* Marx, 1960, *A. pachacamac* Melo-Sampaio, Passos, Prudente, Venegas & Torres-Carvajal, 2021, *A. serranus* Amaral, 1930, *A. torquatus* Duméril, Bibron & Duméril, 1854, *A. touzeti* Schargel, Lamar, Passos, Valencia, Cisneros-Heredia & Campbell, 2013, and *A. trihedrurus* Amaral, 1926. Except for *Atractus serranus*, all other species have dorsal bands, differing from the uniform dorsum of *A. paulus* (Figs 2, 4). In addition, other diagnostic features between *A. paulus* and species with specimens recorded above 600 mm SVL were provided in table 1 of Passos et al. (2010). However, inasmuch as size has evolved independently in various clades (Arteaga et al. 2017; Melo-Sampaio et al. 2019a, 2021a; Arteaga et al. 2022). None of those giant species shares the presence of two apical pits on dorsal scales, so we restrict the comparisons to two species possessing two apical pits on dorsal scales and occurring at high elevations in montane forest of the eastern Andes: *Atractus duboisi* (Boulenger, 1880) and *Atractus orcesi* Savage, 1955 (Figs 5, 6).

We did not directly examine the holotype of *Atractus ecuadorensis* Savage, 1955 and *Atractus resplendens* Werner, 1901, so it is not known whether they have apical pits, likewise, it does not allow us to conclude that these species constitute a natural group with the previous ones (see Fig. 7). Although Arteaga et al. (2022) noticed that a black stripe on a yellow belly is a characteristic shared by *A. duboisi*, *A. discovery*, and *A. orcesi*, they mistakenly assumed that it is absent in *A. resplendens.* This is clearly stated to be present in the description given by Werner (1901).

**Figure 2.** Dorsal pattern of juveniles for comparison: **A** *A. gigas* MEPN 8706 and **B** *A. paulus*.

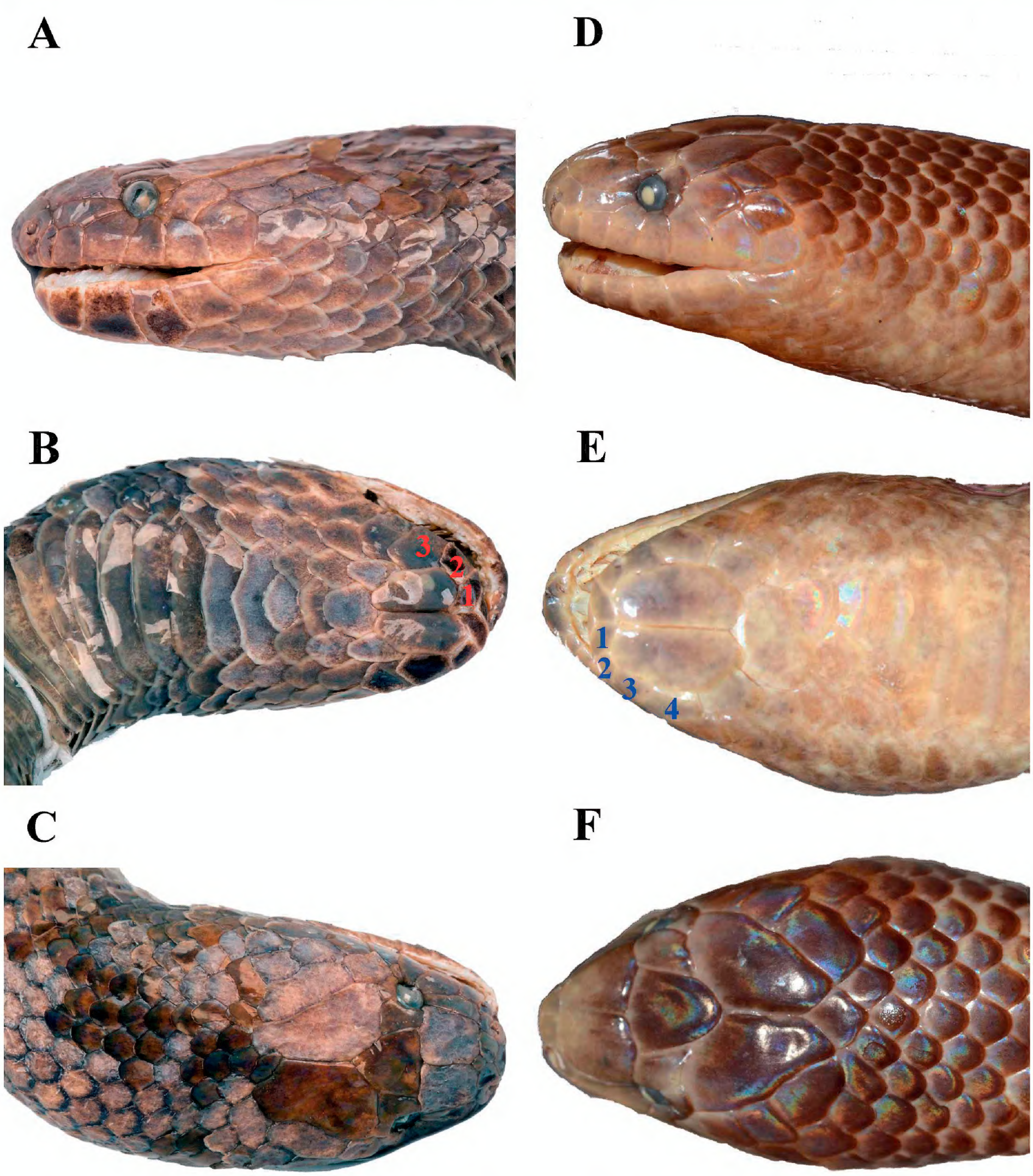


**Figure 3.** Comparison of holotypes head in lateral, ventral and dorsal views. **A–C** *Atractus gigas*; **D–F** *Atractus paulus*. Note the contact of infralabials with chinshield (3 in *A. gigas* versus 4 in *A. paulus*).

*Atractus paulus* differs from *A. duboisi* by having 17 dorsal scale rows, dorsum uniformly reddish in adult specimens, eight supralabials with fourth and fifth entering orbit (vs. 15 dorsal scale rows, seven supralabials with third and fourth entering orbit, adults dark brown or black with yellowish paired paravertebral dots in *A. duboisi*); from *A. orcesi* by having 17 dorsal scale rows, dorsum uniformly reddish in adult specimens (vs. 15 dorsal scale rows, dorsal colour dark brown with a cream- brown occipital band, vertebral and dorsolateral stripes in *Atractus orcesi*).

**Description of the holotype.** An adult female, SVL 830 mm, tail length 83 mm (9.1% of total length); head distinct from body; head length 22.6 mm (2.7% SVL); head width 19.8 mm (87.6% head length); rostral–orbit distance 9.3 mm; nostril–orbit distance 6.8 mm; interorbital distance 10.9 mm; head rounded in lateral view; snout sub-acuminate in dorsal view, truncate in lateral view; canthus rostralis not conspicuous; rostral subtriangular in frontal view, 4.6 mm wide, 3.0 mm high, slightly visible in dorsal view; internasal 2.5 mm long,

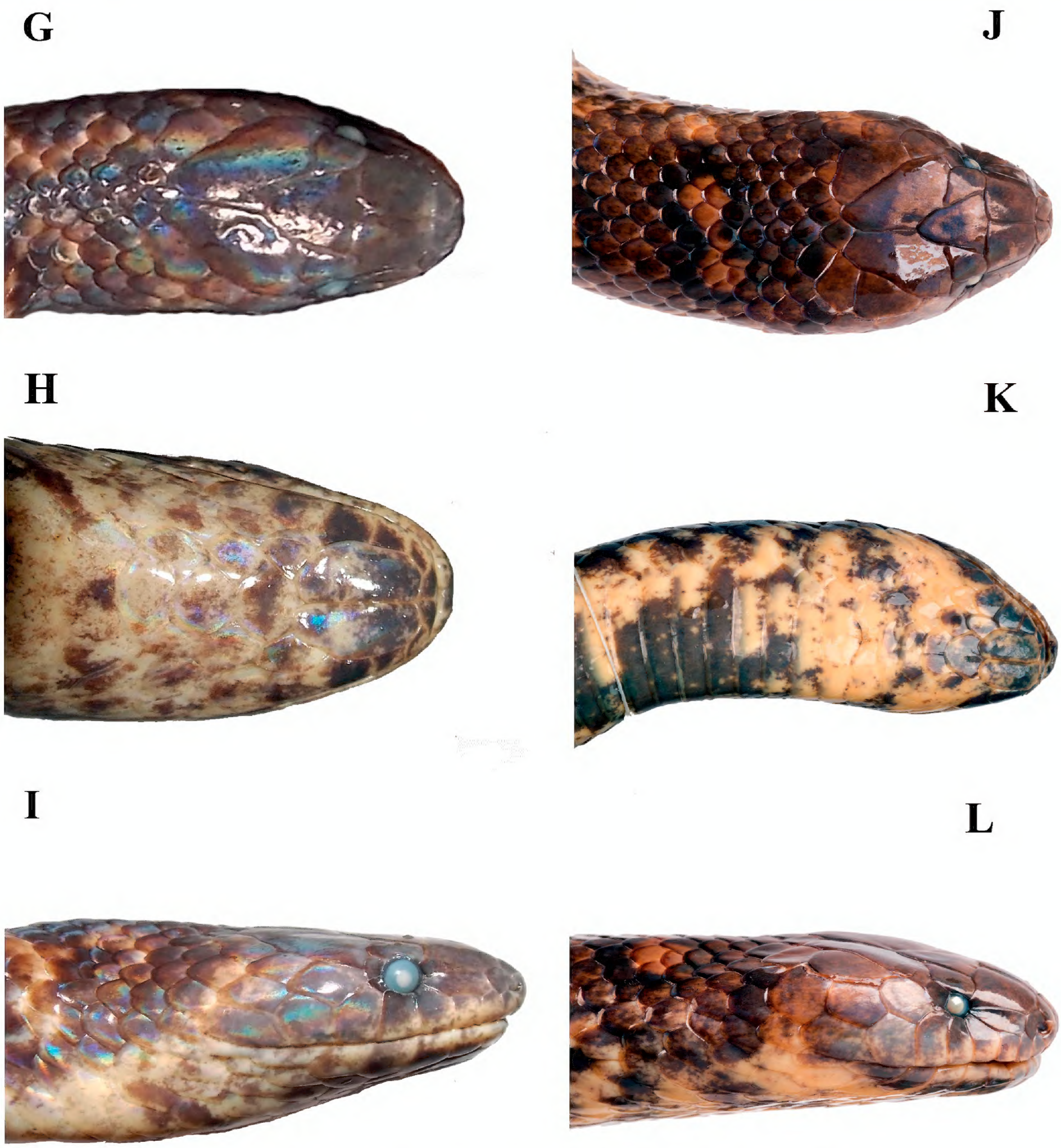


**Figure 4.** Comparison of holotypes head in dorsal, ventral and lateral views. **G–I** *Atractus atlas* and **J–L** *Atractus touzeti*.

2.30 mm wide; internasal suture sinistral with respect to prefrontal suture; prefrontal 6.1 mm long, 4.9 mm wide; supraocular subtrapezoidal, 4.5 mm long, 3.4 mm wide at broadest point; frontal pyramidal, 7.0 mm long, 5.9 mm wide; parietal 10.8 mm long, 7.1 mm wide; nasal entirely divided, nostril well-spaced into both pre- and postnasal; prenasal 2.4 mm high, 1.5 mm long; postnasal 2.6 mm high, 2.5 mm long; loreal 5.0 mm long, 1.9 mm high; second, third and fourth supralabials contacting loreal on left side; third to fifth supralabials contacting loreal on right side; eye diameter 2.9 mm; pupil rounded; two postoculars similar in height, being upper longer than lower; upper postocular 2.2 mm long, 2.7 mm high; lower postocular 1.4 mm long, 1.6 mm high; temporal formula 1+2; first temporal 5.3 mm long, 4.3 mm high; upper posterior temporal, 5.6 mm long, 4.3 mm wide; supralabials nine, fifth and sixth contacting eye on right side, supralabials eight, fourth and fifth contacting eye on left side; first supralabial narrower (1.4 mm wide) than second (1.7 mm wide) and similar in height; third supralabial trapezoidal, similar in height and wider (2.1 mm) than second; sixth (right) and seventh supralabial taller (left) and seventh (right) and eighth longer (left) than remaining supralabials; symphysial subtriangular, 3.1 mm wide, 1.3 mm long; first pair of infralabials preventing contact symphysial–chinshields; infralabials eight (right)

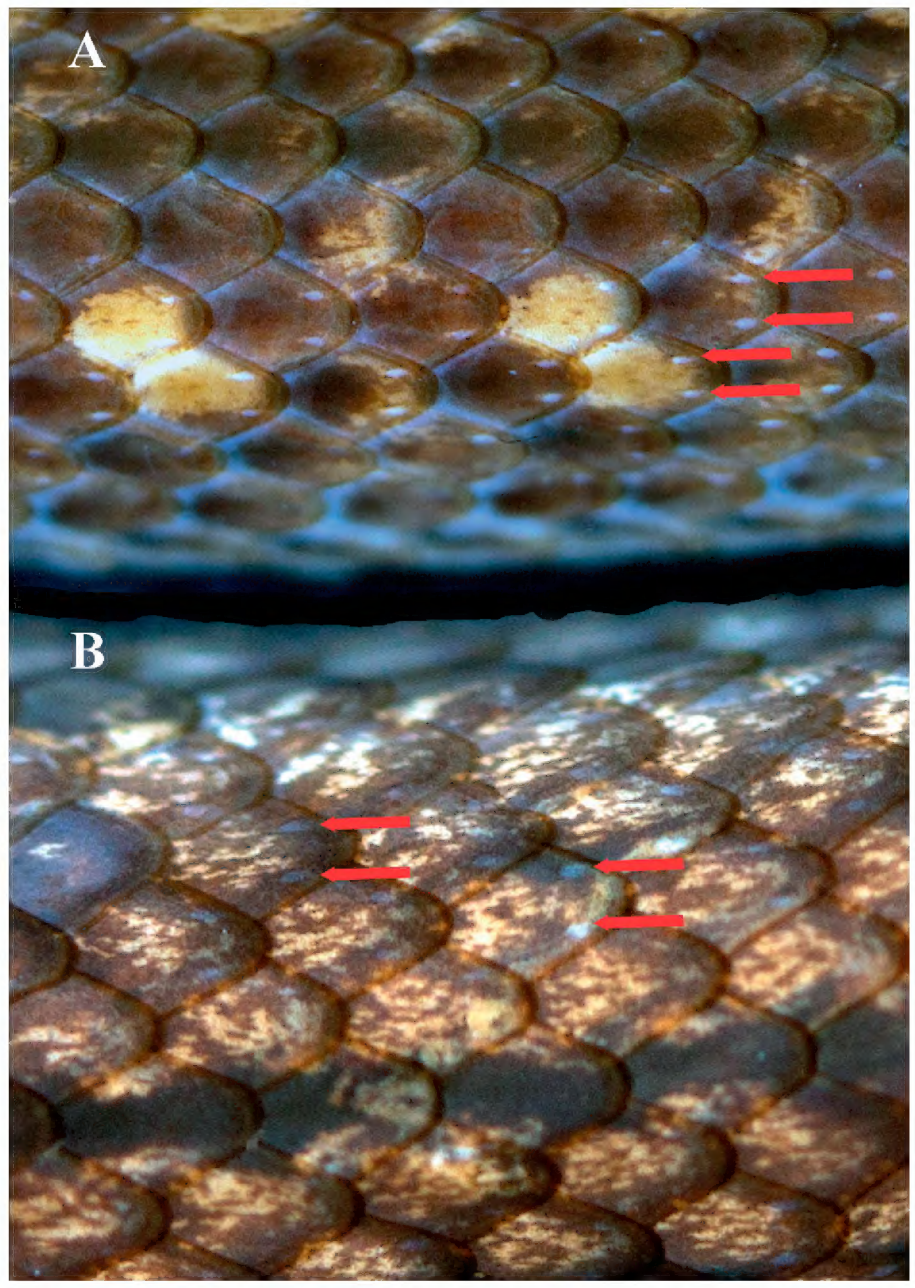


**Figure 5.** Apical pits in dorsal scales indicated by red arrows: **A** *A. duboisi* QCAZ 2759 and **B** *A. orcesi* QCAZ 2779.

and seven (left), first four contacting chinshields; chinshields 8.9 mm long; gular scale rows four; preventrals four; ventrals 167; subcaudals 26/26 respectively from left to right side; dorsal scale rows 17/17/17, with apical pits at level of cloaca; midbody diameter 27.3 mm (3.3% of SVL); caudal spine 3.2 mm long, shorter than last fused subcaudal scale (2.8 mm). Maxillary bone arched upward anteriorly in lateral view, ventral portion curved on anterior and nearly flattened on median to posterior portion; maxillary with eight teeth; teeth angular in cross section, robust at base, narrower at apices, curved posteriorly; lateral process of maxilla well developed (Figs 2, 3). Paratype ZFMK 89147 agrees in most of characters of holotype, differing only in colouration and scale counts (166) in venter.

**Colour in life and preservative.** Passos et al. (2010) described the colouration as follows: dorsum and background of head mostly dark brown. We observed that dorsum and head are Raw umber (colour 23) with gradation to cinnamon in contact internasals-prefrontals (colour 21) becoming cinnamon rufous (colour 31) on snout region; supralabials cinnamon with small invasion of cinnamon rufous; mental and gular regions mostly dark brown, with few cream (colour 12) dots; venter light to dark brown, with few cream to greyish brown dispersed dots (colour 284); underside of tail dark brown. Ontogenetic variation is pronounceable (see fig. 2 of Passos et al. 2010), where juvenile has head and dorsal ground colour of body dark greyish brown to sepia (colour 286), with few dispersed

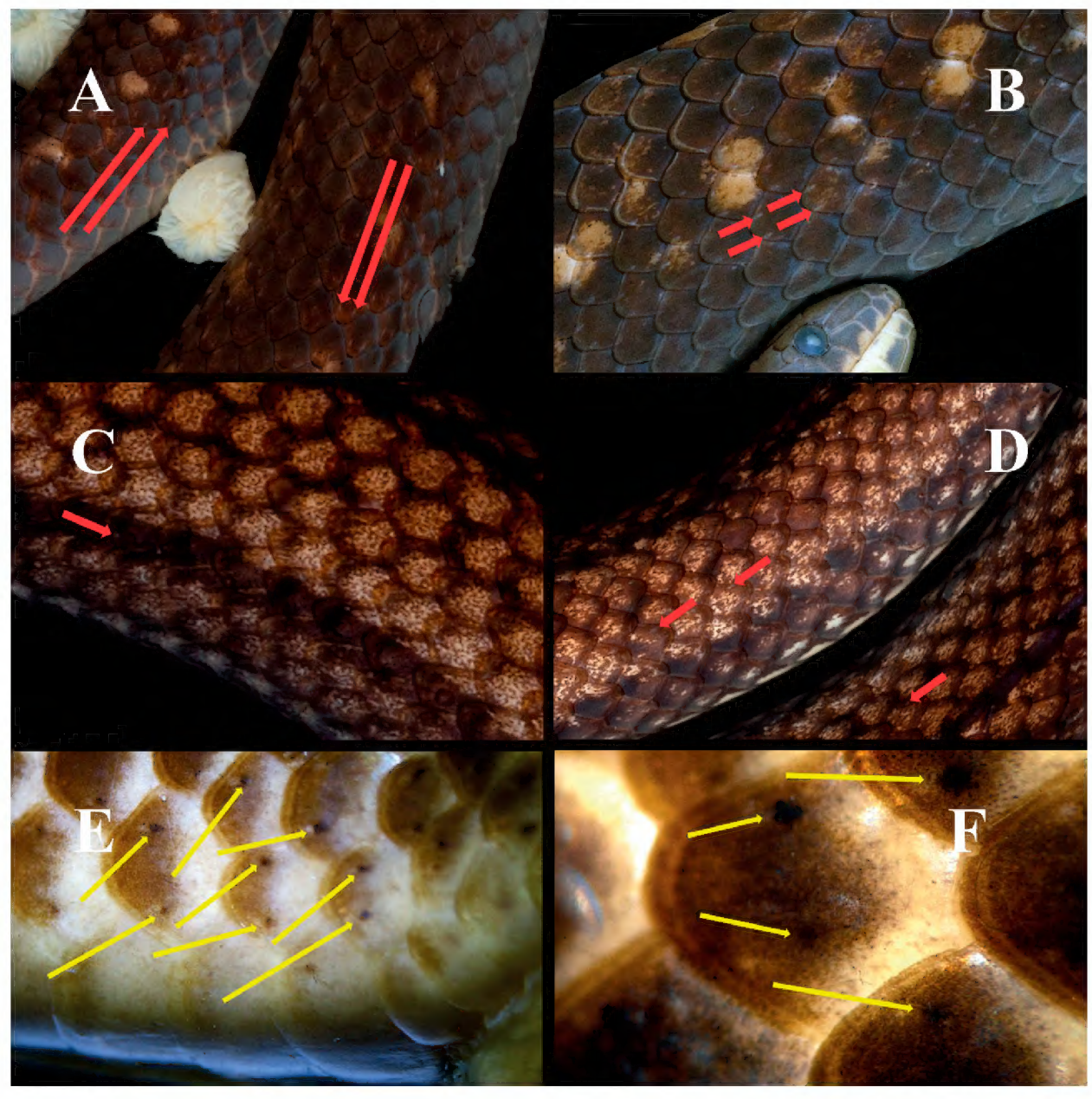


**Figure 6.** Apical pits in dorsal scales indicated by red arrows in **A** *A. duboisi* QCAZ 3302 (QCAZ/bioweb) and **B** *A. duboisi* QCAZ 2801 (QCAZ/bioweb - CC BY-NC-ND 4.0); **C** *A. zgap* QCAZ 5183 (sensu Arteaga et al. 2022) and **D** *A. orcesi* QCAZ 2779. Apical pits indicated by yellow arrows in **E, F** *Atractus paulus* CORBIDI 877.

**Figure 7.** Holotypes: **A** *Atractus resplendens* ZMB 17414 and **B** *Atractus ecuadorensis* FMNH 23529 (Field Museum of Natural History – CC BY-NC 4.0).

buff (colour 5) stains almost forming a nuchal collar, cinnamon to chamois (colour 84) dots or barely distinct bands are present in dorsolateral region of body and tail. Posterior part of chishields and gular region is pale cinnamon (colour 55). Venter is sepia with dispersed pale cinnamon blotches; cloacal region is pale cinnamon; subcaudals sepia with stained pale cinnamon midventrally close to cloaca.

**Distribution and natural history.** The new species is known from two close localities Alto Ihuamaca and El Chaupe, at elevations of 1641–2161 m in the northern portion of the Cordillera Occidental of the Andes, San Ignacio province, Cajamarca department, Peru (Fig. 8). Both localities are in agricultural areas with coffee plantations and pastures for cattle ranching with scattered small patches of montane forest and secondary vegetation. According to Passos et al. (2010), the adult female holotype was collected by day crossing a trail at the forest edge in an open area and the juvenile paratype inactive under a log near a coffee plantation. The holotype contained 12 eggs in the oviduct, measuring 30.4–36.3 mm (X = 33.7 mm) length and 14.5-16.3 mm (X = 15.5 mm) width (Passos et al. 2010).

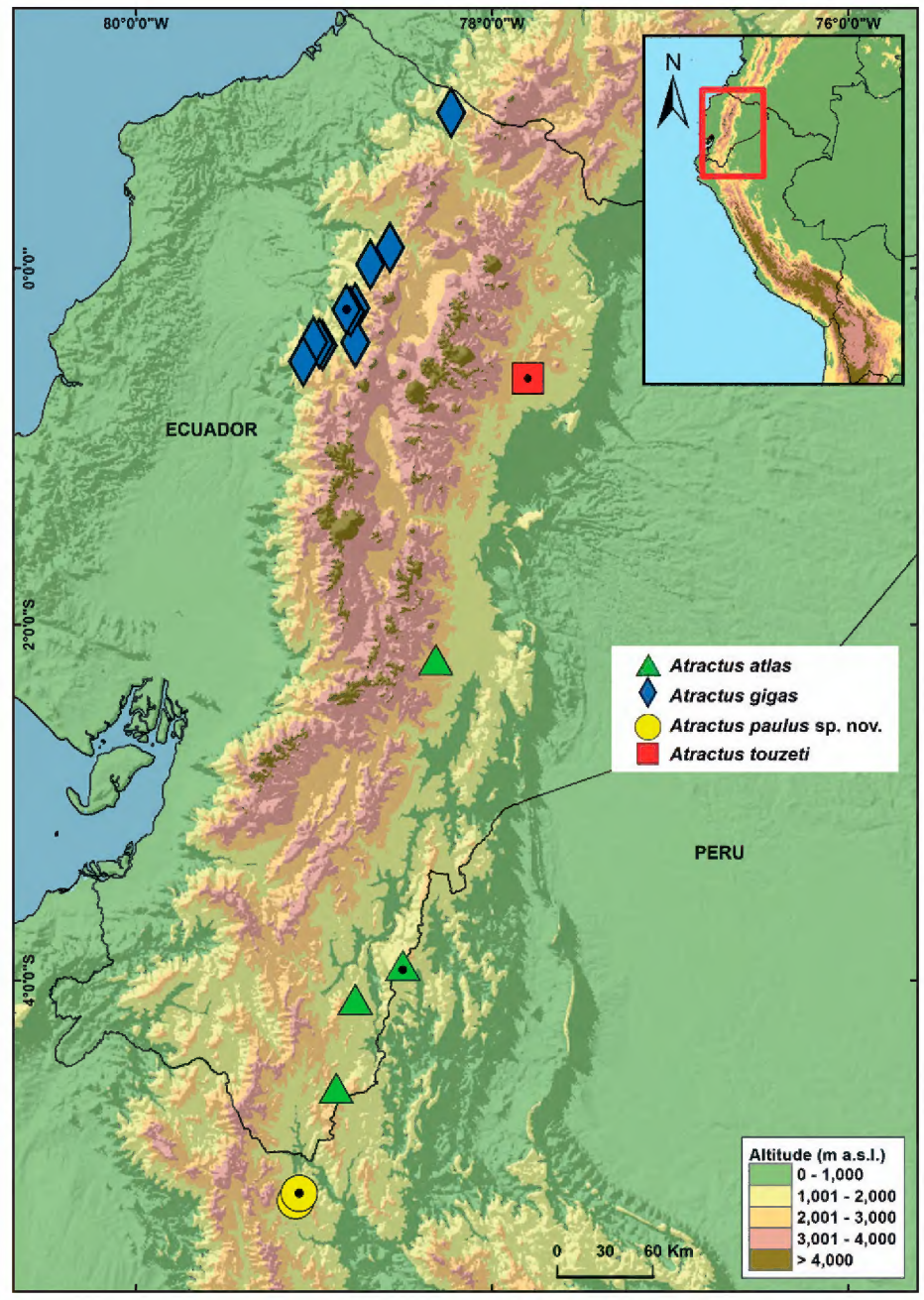


**Figure 8.** Geographical distribution of giant groundsnakes. Triangles = *Atractus atlas*. Diamonds = *Atractus gigas*. Circles = *Atractus paulus*. Square = *Atractus touzeti*. Type localities are filled with a dot.

**Etymology.** The species epithet "paulus" is a Latin word being patronym for our friend Paulo Gustavo Homem Passos. Dr. Paulo Passos has described more than 34 *Atractus* species, approximately one-fifth of the astonishing diversity of this complex genus. The Latin word "Paulus" also means "small" and thus, we also refer to the type series composed only by the holotype and paratype.

**Remarks.** The montane forest below 2000 m in the San Ignacio province has almost disappeared owing to agricultural activities. Only scattered patches of montane forest and secondary vegetation can be observed in the landscape. The National Sanctuary Tabaconas Namballe is between approximately 5 and 9 km in a straight line from the localities of *Atractus paulus* preserve forests from 2000 m. Even other protected private areas in San Ignacio possess most of their natural surfaces above 2000 m.

However, due to scarcity of knowledge about the distribution of this new species, especially its altitudinal range, we could not objectively propose a conservation category based on the IUCN criteria, but due to the levels of habitat destruction in the area efforts should be allocated for the conservation status of this species to be rapidly reassessed.

## Discussion

The description of *Atractus paulus* raises questions and concerns about the lack of attention to detail in the use of some traditional morphological characteristics in snake taxonomy, such as the presence of apical pits, within the genus *Atractus*. The interest in making taxonomy increasingly integrative with the inclusion of molecular data combined with the need to publish data faster has minimized the use of informative and well-known character systems such as hemipenial morphology (Passos et al. 2012). Consequently, diagnostic comparisons are becoming increasingly basic and inadequate (see Arteaga et al. 2017, 2022).

Passos et al. (2009) removed *Atractus duboisi* and *A. orcesi* from the synonymy of *Atractus occiptoalbus* (Jan, 1862) as proposed by Savage (1960). Passos et al. (2009: 391–392) give the following diagnosis for *Atractus duboisi*: 15/15/15 dorsal scale rows without apical pits, supra-anal tubercles and keels; usually eight supralabials, with 4–5$^{th}$ contacting orbit; usually seven infralabials; seven maxillary teeth; usually four series of gular rows; subcaudals 23–26 in males. However, after careful analysis of the specimens of *A. duboisi*, we found that all specimens possess apical pits (often more visible near the cloaca in females, sometimes distributed throughout the body, except in the first two dorsal scales and vertebral row), usually seven supralabials in males, eight maxillary teeth and 30–35 subcaudals in males similar to reported in Boulenger (1894). Furthermore, Passos et al. (2009) in the revalidation of *Atractus orcesi* Savage, 1955, did not mention presence of apical pits in this species. After examining specimens, we found that apical pits are also present (Figs 5, 6). The ornamentation of the scales (with apical pits, keels and tubercles), which was an innovative character in the positioning of species in the genus *Atractus* in the past (Gasc and Rodrigues 1979; Hoogmoed 1980), was neglected for a long time, but finally received attention again with the publication of Passos et al. (2013) on *A. caxiuana*; Fraga et al. (2017) on *Atractus riveroi*; and Passos et al. (2022) on *Atractus badius*, and was also very important for this study.

Arteaga et al. (2017), provided the first molecular phylogeny with mitochondrial genes including *A. duboisi*, *A. ecuadorensis* Savage, 1955 and *A. resplendens* Werner, 1901. Although *A. ecuadorensis* and *A. resplendens* are rare species very little has been discussed about their morphological variation. Arteaga et al. (2022) expanded their phylogeny to include *A. orcesi* and and a new species, *A. discovery*, and retrieved both species nested in a clade sister to *A. duboisi* + *A. resplendens*, respectively.

Based on previous phylogenetic results and the presence of apical pits, herein we name the *Atractus duboisi* group, including the following species: *A. discovery*, *A. duboisi*, *A. orcesi*, and *A. paulus*. *Atractus discovery* is tentatively assigned to this group based on molecular positioning retrieved in Arteaga et al. (2022). We refrain to include *A. ecuadorensis* and *A. resplendens* because we are unable to check the vouchers (DHMECN 5105 and MZUTI 3996 respectively) utilized by Arteaga et al. (2017). Complementarily, a recent study by Passos et al. (2022) shows that many sequences presented in Arteaga's work included misidentifications, but do not affect or influence the decisions made here. Furthermore, Arteaga et al. (2022) criticized Passos' work but themselves concede that some reidentifications were warranted by recognizing synonymy of one species that they described. On the other hand, two juvenile specimens QCAZ 5183 (Fig. 6C) and QCAZ 12666 described as paratypes of *Atractus zgap* have apical pits and therefore verification of the condition in the holotype (ZSFQ 4946) is crucial to understanding interspecific relationships of this group if they are not conspecific. Additionally, the status of *A. discovery* needs to be assessed through exhaustive comparison with *A. resplendens*, comparing the hemipenial morphology of both species. Despite that both species were recovered as sibling species and males are available in museum collections, preparation of hemipenes was not done.

Recent taxonomic revisions have improved knowledge about *Atractus* species described based on holotypes or small type series (Passos et al. 2013; Schargel et al. 2013; Köhler and Kieckbusch 2014; Arteaga et al. 2017, 2022; Melo-Sampaio et al. 2019; Passos et al. 2019a, b; Melo-Sampaio et al. 2021a). As long as there is no systematic collection in the Andes, the rate of discovery of new species of reptiles will always be a product of serendipity so a better understanding of snake relationships in a vicarious context like the Andes is still in its infancy (see Melo-Sampaio et al. 2021a, b). However, the main forces that impede taxonomic progress in *Atractus* are: the large number of synonyms, the inaccurate description of species, the unjustified revalidation of synonymized species, the low representativeness in museums and the sample gaps established by the difficulty of access to the collection sites, financing or even for geopolitical and bureaucratic issues that do not allow the joint effort of researchers.

## Acknowledgments

We thank Omar Torres-Carvajal and Fernando Ayala-Varela (QCAZ), Ana Almendáriz (MEPN), Mario Yánez-Muñoz (DHMECN), Frank Tillack (ZMB), Juan C. Chávez-Arribasplata and Claudia Koch (ZFMK), David Kizirian and Lauren Vonnahme (AMNH) for sending photos and/or allowing us to examine specimens under their care. PRMS thanks Paulo Passos for doctoral guidance, friendship, knowledge and data shared about Neotropical snakes, especially *Atractus*. Special thanks to editor Oliver Hawlitschek. We are also indebted with William W. Lamar for the early review of the manuscript and Walter Schargel for his valuable comments on it.

## References

Arteaga A, Mebert K, Valencia JH, Cisneros-Heredia DF, Peñafiel N, Reyes-Puig C, Vieira-Fernandes JL, Guayasamin JM (2017)

Molecular phylogeny of *Atractus* (Serpentes, Dipsadidae), with emphasis on Ecuadorian species and the description of three new taxa. ZooKeys 661: 91–123. https://doi.org/10.3897/zookeys.661.11224

Arteaga A, Quezada A, Vieira J, Guayasamin JM (2022) Leaving no stone unturned: three additional new species of *Atractus* ground snakes (Serpentes, Colubridae) from Ecuador discovered using a biogeographical approach. ZooKeys 1121: 175–210. https://doi.org/10.3897/zookeys.1121.86539

Boulenger GA (1880) Reptiles et Batraciens recueillis par M. Emile de Ville dans les Andes de l'équateur. Bulletin de la Société Zoologique de France 5: 41–48.

Boulenger GA (1894) Catalogue of the snakes in the British Museum (Natural History). Vol. II. Containing the Conclusion of the Colubridæ Aglyphæ. British Museum Natural History, London, [xi] 382 pp.

Dowling HG (1951) A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1: 97–99.

Fraga R, Almeida AP, Moraes LJCL, Gordo M, Pirani R, Zamora RR, Carvalho VT, Passos P, Werneck FP (2017) Narrow endemism or insufficient sampling? geographic range extension and morphological variation of the poorly known *Atractus riveroi* Roze, 1961 (Serpentes: Dipsadidae). Herpetological Review 48(2): 281–284.

Gasc JP, Rodrigues MT (1979) Une nouvelle espece du genre *Atractus* (Colubridae, Serpentes) de la Guyane française. Bulletin du Museum National D'histoire Naturelle Section A Zoologie Biologie et Ecologie Animales 4(2): 547–557. https://doi.org/10.5962/p.283210

Hoogmoed MS (1980) Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the herpetofauna of Surinam: VII. Zoologische Verhandelingen 175(1): 3–47. https://doi.org/10.1163/156853881X00384

Jowers MJ, Schargel WE, Muñoz-Mérida A, Sánchez-Ramírez S, Weber JC, Faria JF, Harris DJ, Murphy JC (2021) The enigmatic biogeography of Tobago's marooned relics: The case study of a fossorial snake (Squamata, Dipsadidae). Journal of Zoological Systematics and Evolutionary Research 59(6): 1382–1389. https://doi.org/10.1111/jzs.12509

Köhler G (2012) Color Catalogue for Field Biologists. Herpeton, Offenbach, 49 pp.

Köhler G, Kieckbusch M (2014) Two new species of *Atractus* from Colombia (Reptilia, Squamata, Dipsadidae). Zootaxa 3872(3): 291–300. https://doi.org/10.11646/zootaxa.3872.3.5

Marx H (1960) A new colubrid snake of the genus *Atractus*. Fieldiana Zoology 39(38): 411–413. https://doi.org/10.5962/bhl.title.3562

Melo-Sampaio PR, Passos P, Fouquet A, Prudente ALC, Torres-Carvajal O (2019) Systematic review of *Atractus schach* (Serpentes: Dipsadidae) species complex from the Guiana Shield with description of three new species. Systematics and Biodiversity 17: 207–229. https://doi.org/10.1080/14772000.2019.1611674

Melo-Sampaio PR, Passos P, Prudente ALC, Venegas PJ, Torres-Carvajal O (2021a) Systematic review of the polychromatic ground snakes *Atractus snethlageae* complex reveals four new species from threatened environments. Journal of Zoological Systematics and Evolutionary Research 59: 718–747. https://doi.org/10.1111/jzs.12453

Melo-Sampaio PR, Passos P, Martins AR, Jennings WB, Moura-Leite JC, Morato SAA, Venegas PJ, Chávez G, Venâncio NM, Souza MB (2021b) A phantom on the trees: Integrative taxonomy supports a reappraisal of rear-fanged snakes classification (Dipsadidae: Philodryadini). Zoologischer Anzeiger 290: 19–39. https://doi.org/10.1016/j.jcz.2020.10.008

Meneses-Pelayo E, Passos P (2019) New polychromatic species of *Atractus* (Serpentes: Dipsadidae) from the Eastern portion of the Colombian Andes. Copeia 107(2): 250–261. https://doi.org/10.1643/CH-18-163

Murphy JC, Salvi D, Braswell AL, Jowers MJ (2019) Phylogenetic position and biogeography of the three-lined snake *Atractus trilineatus* (Squamata, Dipsadidae) in the Eastern Caribbean. Herpetologica 75: 247–253. https://doi.org/10.1655/D-18-00043

Myers CW, Schargel WE (2006) Morphological extremes–two new snakes of the genus *Atractus* from northwestern South America (Colubridae: Dipsadinae). American Museum Novitates 3532: 1–13. https://doi.org/10.1206/0003-0082(2006)3532[1:MENSOT]2.0.CO;2

Passos P, Mueses-Cisneros JJ, Lynch JD, Fernandes R (2009) Pacific lowland snakes of the genus *Atractus* (Serpentes: Dipsadidae), with description of three new species. Zootaxa 2293: 1–34. https://doi.org/10.11646/zootaxa.2293.1.1

Passos P, Dobiey M, Venegas PJ (2010) Variation and natural history notes on giant groundsnake, *Atractus gigas* (Serpentes: Dipsadidae). South American Journal of Herpetology 5(2): 73–82. https://doi.org/10.2994/057.005.0201

Passos P, Cisneros-Heredia DF, Rivera DE, Aguilar C, Schargel WE (2012) Rediscovery of *Atractus microrhynchus* and reappraisal of the taxonomic status of *A. emersoni* and *A. natans* (Serpentes: Dipsadidae). Herpetologica 68: 375–392. https://doi.org/10.1655/HERPETOLOGICA-D-11-00078.1

Passos P, Ramos LO, Pinna PH, Prudente ALC (2013) Morphological variation and affinities of the poorly known snake *Atractus caxiuana* (Serpentes: Dipsadidae). Zootaxa 3745(1): 35–48. https://doi.org/10.11646/zootaxa.3745.1.3

Passos P, Prudente ALC, Lynch JD (2016) Redescription of *Atractus punctiventris* and description of two new *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. Herpetological Monographs 30(1): 1–20. https://doi.org/10.1655/HERPMONOGRAPHS-D-14-00009

Passos P, Azevedo JAR, Nogueira CC, Fernandes R, Sawaya RJ (2019a) An integrated approach to delimit species in the puzzling *Atractus emmeli* complex (Serpentes: Dipsadidae). Herpetological Monographs 33(1): 1–25. https://doi.org/10.1655/0733-1347-33.1.1

Passos P, Scanferla A, Melo-Sampaio PR, Brito J, Almendáriz A (2019b) A giant on the ground: another large-bodied *Atractus* (Serpentes: Dipsadinae) from Ecuadorian Andes, with comments on the dietary specializations of the goo-eaters snakes. Anais da Academia Brasileira de Ciências 91: e20170976. https://doi.org/10.1590/0001-3765201820 170976

Passos P, Melo-Sampaio PR, Ramos LO, Grazziotin FG, Fouquet A, Torres-Carvajal O (2022) When the tail shakes the snake: phylogenetic affinities and morphology of *Atractus badius* (Serpentes: Dipsadidae), reveals some current pitfalls on the snake's systematics. Anais da Academia Brasileira de Ciências 94(1): e20191254. https://doi.org/10.1590/0001-3765202220191254

Peters JA (1964) Dictionary of Herpetology. Hafner, New York, 392 pp.

Savage JM (1955) Descriptions of new colubrid snakes, genus *Atractus*, from Ecuador. Proceedings of Biological Society of Washington 68: 11–20.

Savage JM (1960) A revision of the Ecuadorian snakes of the genus *Atractus*. Miscellaneous Publications, Museum of Zoology, University of Michigan 112: 1–86.

Schargel WE, Lamar WW, Passos P, Valencia JH, Cisneros-Heredia DF, Campbell JA (2013) A new giant *Atractus* (Serpentes: Dipsadidae) from Ecuador, with notes on some other large Amazonian congeners. Zootaxa 3721(5): 455–474. https://doi.org/10.11646/zootaxa.3721.5.2

Silva-Haad JJ (2004) Las serpientes del género *Atractus* Wagler, 1828 (Colubridae; Xenodontinae) en la Amazonia colombiana. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales 28(108): 409–446.

Tolhurst B, Peck M, Morales JN, Cane T, Recchio I (2010) Extended distribution of a recently described dipsadine colubrid snake: *Atractus gigas*. Herpetology Notes 3: 73–75.

Uetz P, Freed P, Aguilar R, Reyes F, Hošek J [Eds] (2023) The Reptile Database. http://www.reptile-database.org [Accessed on 23 May 2023]

Werner F (1901) Ueber Reptilien und Batrachier aus Ecuador und Neu-Guinea. Verhandlungen der Kaiserlich-Koniglichen Zoologisch-Botanischen Gesellschaft in Wien 51: 593–614. https://doi.org/10.5962/bhl.part.4586

# Appendix 1

*Atractus atlas* (*n* = 4). ECUADOR: Zamora-Chinchipe: Paquisha: (MEPN 14203, holotype), Parroquía Guayzimi: (DHMECN 2972, paratype). Morona-Santiago: Reserva Biológica Cerro Plateado: (QCAZ 14946, paratype); Zúñac: (DHMECN 12361, paratype).

*Atractus duboisi* (*n* = 63): ECUADOR: Napo: Baeza: QCAZ 1063, QCAZ 1234–1241, QCAZ 2095–2097, QCAZ 2103, QCAZ 3559, QCAZ 4110, QCAZ 4156. Cosanga: QCAZ 906, QCAZ 2098, QCAZ 2106–2107, QCAZ 2759, QCAZ 2797–2806, QCAZ 3290, QCAZ 3302, QCAZ 3346–3350, QCAZ 3707, QCAZ 3709, QCAZ 5469, QCAZ 6545, QCAZ 8797, QCAZ 9831, QCAZ 10567–10568, QCAZ 10683, QCAZ 10685, QCAZ 10966–10969, QCAZ 11203. Rio Hollín, Via Loreto: QCAZ 2104. Carretera Baeza-Quito: QCAZ 4195, QCAZ 4201. Cuyuja: QCAZ 3542, QCAZ 3543, QCAZ 13262. Mospa: QCAZ 12598. Papallacta: QCAZ 11027–11029.

*Atractus gaigeae* (*n* = 1): ECUADOR: Orellana: Dayuma: QCAZ 11009.

*Atractus gigas* (*n* = 5): ECUADOR: Cotopaxi: (FHGO 194, holotype), Las Pampas: QCAZ 662. Pichincha: Chiriboga: QCAZ 1. Piso Tropical Oriental (error): without specific data: (MEPN 8706, MEPN 8718).

*Atractus nigricaudus* (*n* = 4): PERU: Pasco: Oxapampa: MUSM 17761, Parque Nacional Yanachaga-Chemillén: MUSM 31139. No data: MUSM 23467, MUSM 23500.

*Atractus orcesi* (*n* = 5): ECUADOR: Morona-Santiago: Río Hollin: QCAZ 6268, General Leonidas Plaza: QCAZ 7000, QCAZ 9184, QCAZ 9666. Sucumbíos: La Bonita: QCAZ 2779.

*Atractus pachacamac* (*n* = 28): ECUADOR: Napo: Sumaco Wildlife Sanctuary: QCAZ 12630 (holotype), QCAZ 11986, QCAZ 12804, QCAZ 10639, QCAZ 16083 (paratypes); Morona Santiago: General Proaño: MEPN 11454–11455 (paratypes); Cotundo: QCAZ 11075 (paratype); Taisha: Makuma, Paatim Shuar Center: FHGO 10080 (paratype). Napo: Gonzalo Pizarro: El Reventador: DHMECN 11556 (paratype); El Chaco: Sardinas: QCAZ 1493 (paratype); Chontapunta: Sumac Sacha FHGO 2178 (paratype). Orellana: Dayuma: MEPN 7358 (paratype); Joya de los Sachas: San Sebastian del Coca: MEPN 11701 (paratype); Nuevo Paraíso: Village Juan Pablo II: MEPN 5471 (paratype); Aguarico: MEPN 10548 (paratype); Yasuní National Park: QCAZ 10614 (paratype). Pastaza: Villano: Kurintza: QCAZ 8278, QCAZ 8367, QCAZ 11833 (paratypes). Sucumbíos: Lago Agrio: El Eno: FHGO 5813 (paratype). Zamora-Chinchipe: Yanzatza: Los Encuentros: QCAZ 15174, MECN 8437 (paratypes); Reserva Natural Maycu: QCAZ 15414 (paratype); El Zarza: QCAZ 15537 (paratype); El Pangui: Concesión Minera Princesa: MECN 13078 (paratype). PERU: Loreto: Datem del Marañon: Cahuapana: CORBIDI 13797 (paratype); Maynas: Güeppi: CORBIDI 167 (paratype).

*Atractus resplendens* (*n* = 3): ECUADOR: no specific locality, probably Llanganate: ZMB 17414 (holotype). No specific locality: AMNH-R 35932, AMNH-R 28787 (photographs).

*Atractus torquatus* (*n* = 7): BRAZIL: Amazonas: Rio Marari: MZUSP 14281. Rondônia: Porto Velho: MZUSP 18899. Roraima: Parque Nacional do Viruá: INPA-H 28565, INPA-H 28567, INPA-H 28569. SURINAME: Sipaliwini: AF 2281. PERU: Loreto: Estirón: MZUSP 4380.

*Atractus typhon* (*n* = 4): ECUADOR: Esmeraldas: Reserva Tesoro Escondido: QCAZR 14982–14984, QCAZR 14989.

*Atractus ukupacha* (*n* = 22): ECUADOR: Napo: El Chaco: QCAZ 12504 (holotype), QCAZ 4047 (paratype); El Reventador: QCAZ 444, MNRJ 24596 (paratypes); San Francisco de Borja: MNRJ 24597, QCAZ 1606, QCAZ 12490, QCAZ 12596, DHMECN 80 (paratypes); Sardinas: QCAZ 1494 (paratype); Quijos: Santa Rosa: QCAZ 12715 (paratype); San Rafael, San Rafael stream QCAZ 0004, QCAZ 3256 (paratypes); Puerto Misahuallí: Reserva Biológica Jatún Sacha: QCAZ 3476–3477 (paratypes); Cosanga: QCAZ 11202 (paratype); Piedra Fina: QCAZ 4812, QCAZ 4942, QCAZ 4943, QCAZ 4944, (paratypes). Orellana: San José de Payamino: QCAZ 11651–11652, (paratypes).

*Atractus zgap* (*n* = 2): ECUADOR: Napo: El Chaco: QCAZ 5183 (paratype), San Francisco de Borja: QCAZ 12666 (paratype) (photographs).